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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)

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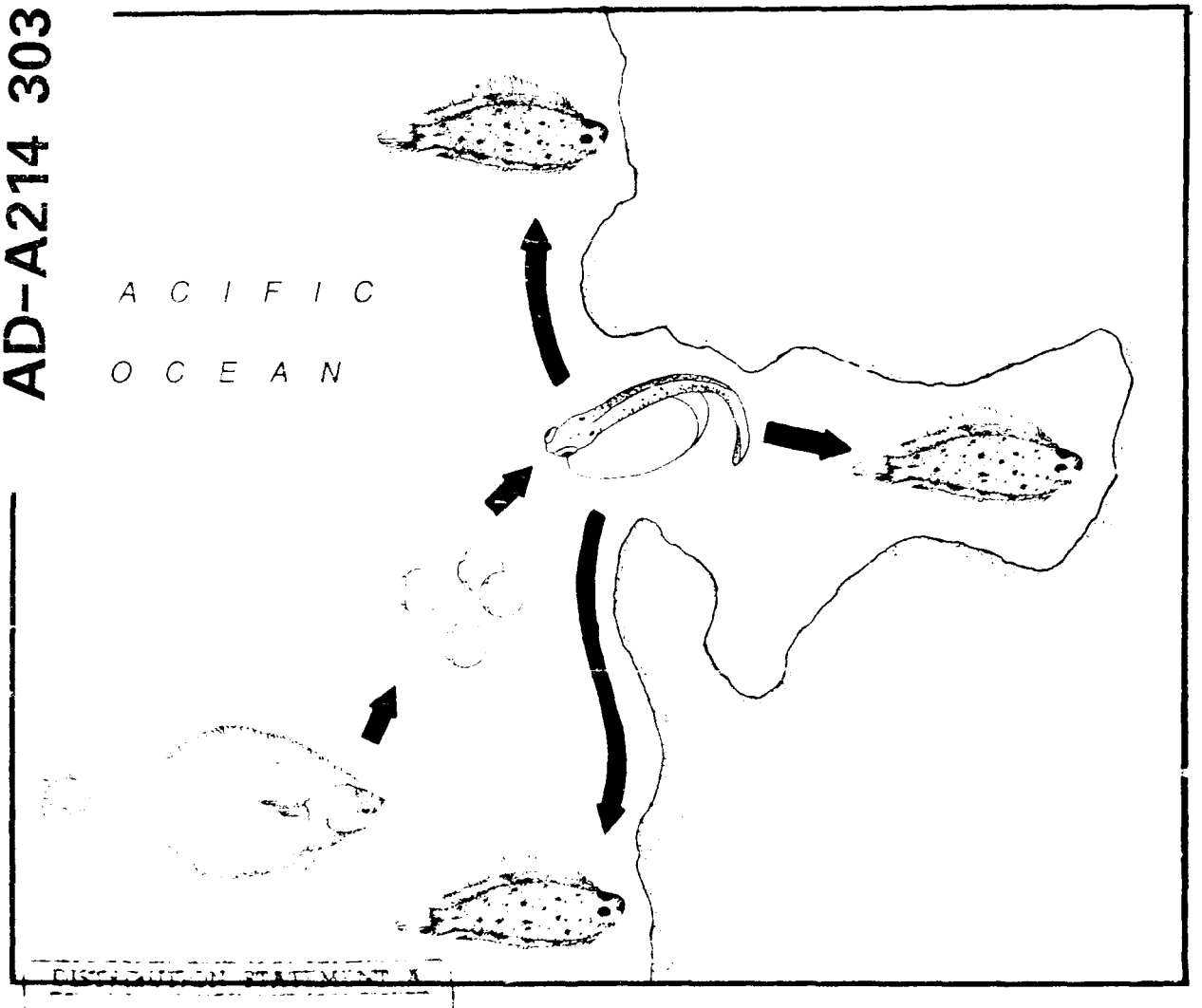

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)

ENGLISH SOLE

by

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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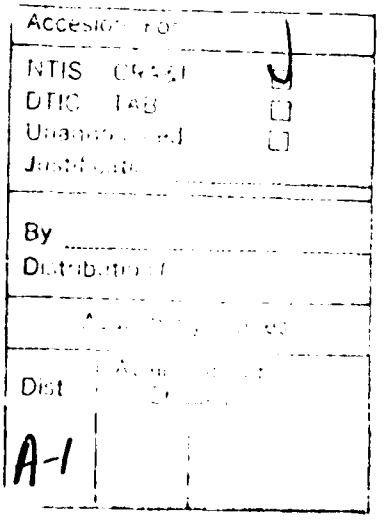

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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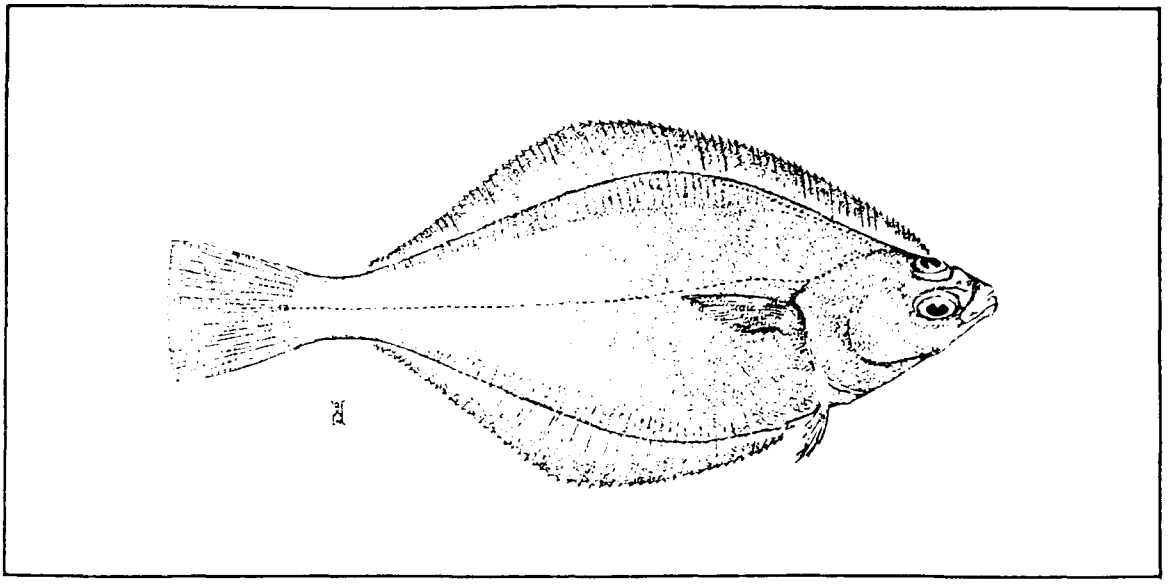

Figure 1. English sole (from Hart 1973).

ENGLISH SOLE

NOMENCLATURE/TAXONOMY/RANGE

Scientific name ... Parophrys vetulus (Girard)
Common name ..... English sole (Figure 1)
Other names ..... This species is known in Canada as the lemon sole and has been called the point sole (for its pointed head) in California. It is believed that specimens that had been previously placed in the species Isopsetta ischyra are actually hybrids of P. vetulus and Platichthys stellatus (Hart 1973).
Class ..... Osteichthyes
Order ..... Pleuronectiformes
Family ..... Pleuronectidae

Geographic range: English sole are known from Sebastian Vizcaino Bay, Baja California, Mexico (lat. 28° 30' N, long. 115° 00' W) to Unimak Island, Alaska (lat. 54°30' N, long. 164° W) and occur in commercial quantities from Santa Barbara, California, to northern Hecate Strait, British Columbia (Alderdice and Forrester 1968). Depth distribution is from the surfline to 550 m (Hart 1973) but it is uncommon at depths greater than 146 m (Demory et al. 1976; Barss et al. 1977). Commercial abundances occur between 37 m and 126 m (Forrester 1969a). Alderdice and Forrester (1968) suggested that the influence of water temperature on egg viability may limit the boundaries of commercially exploitable populations as well as the boundaries of geographic distribution. The distribution of P. vetulus in the Pacific Northwest region is shown in Figure 2.

MORPHOLOGY/IDENTIFICATION AIDS

Body elongate, much compressed, dextral (eyes on the right side). Head slender, with bluntly pointed snout. Mouth terminal, small, asymmetrical, with narrow gape; jaws and teeth strongest on blind side.

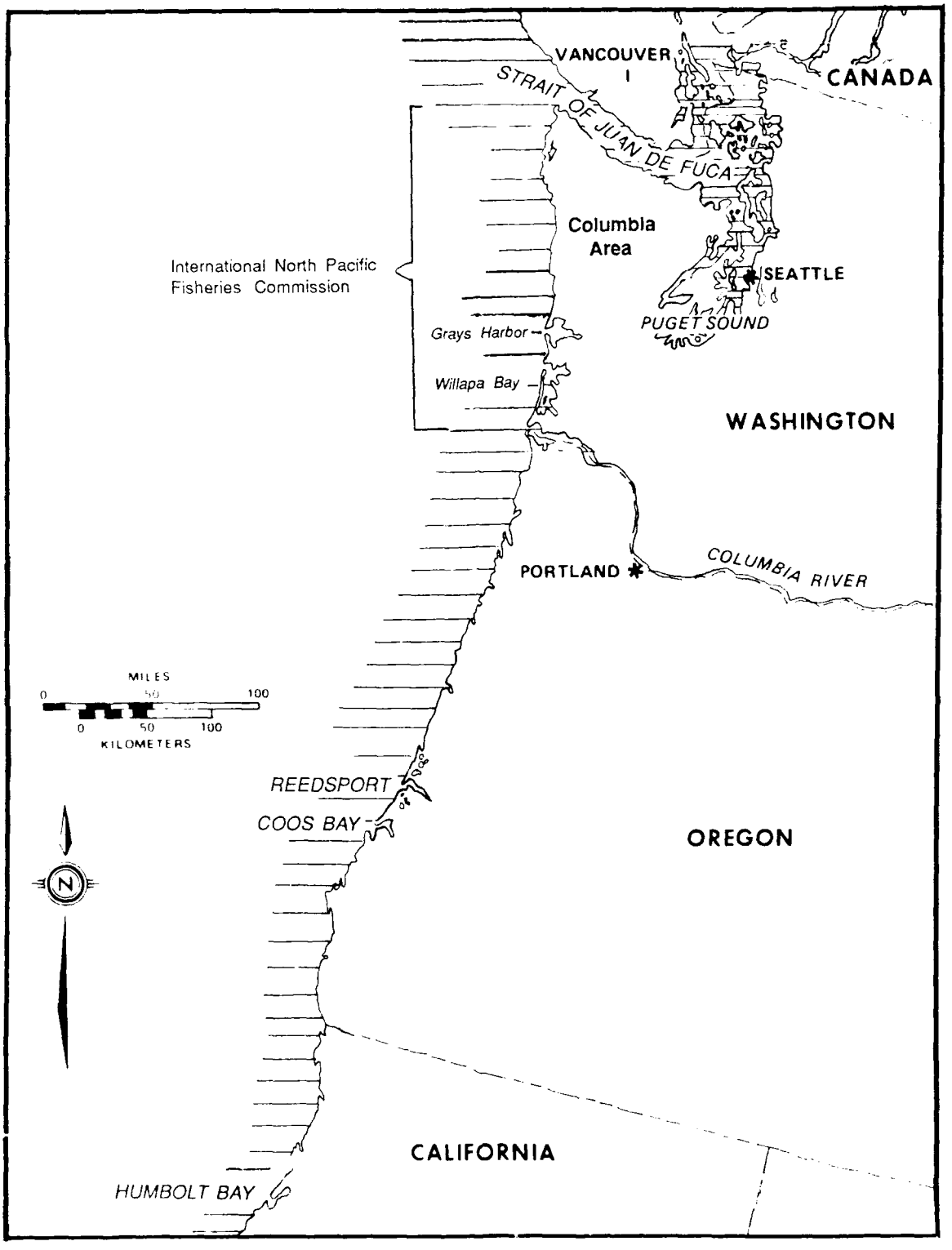

Figure 2. Distribution of the English sole in the Pacific Northwest Region.

Maxillary extends to forward part of lower eye. Eyes large, upper somewhat posterior to lower, entering profile. Interorbital space narrow, ridge high. Dorsal with one spine and 72 to 92 rays, originates above middle of upper eye; anal, 54 to 72 rays, exposed spine before fin; pelvic, 6 rays, thoracic; pectorals tend to be pointed; caudal imperfectly truncate. Scales imbricated, cycloid anteriorly, ctenoid posteriorly. Lateral line, 89 to 105 scales, slightly decurved then straight, dorsal branch long, close to dorsal fin, extends to point over pectoral fin. Color, uniform brown to yellow-brown on eyed side; pale yellow to white on blind side, tinged with reddish brown, particularly on head. Young variously colored gray to brown, minutely spotted, often with sandy appearance on eyed surface (see Misitano 1976 for photos); often with two yellow lines on blind side at bases of dorsal and anal fins. Total length (TL) to 57 cm in females, 47 cm in males.

Distinguished from other flatfishes by a combination of pointed head, long dorsal branch of lateral line, and smooth anterior/rough posterior scale pattern. The above description was abstracted almost entirely from Clemens and Wilby (1961) and Hart (1973).

REASONS FOR INCLUSION IN SERIES

Barss (1976) wrote that among flatfishes coastwide, the catch of English sole was exceeded only by that of the Dover sole and sometimes the Petrale sole. Annual coastwide landings (from California to British Columbia, round weight) averaged 5,141 metric tons (t) from 1971 to 1980 with a peak of 6,680 t in 1976 (Lynde 1986). As in many coastal marine fishes, the juveniles of P. vetulus depend on shallow, nearshore habitats as nursery grounds. Ketchen (1956), in fact, attributed the scarcity of English sole in northern British Columbia to a lack of suitable nursery grounds. During early spring and summer, juvenile English sole are the most abundant flatfish in many Pacific coastal embayments and estuaries (Yoklavich 1982). Barss (1976) suggested that English sole could benefit from protected nursery areas.

My own favorite "reason for inclusion" was stated by Clemens and Wilby (1961): "This is the choicest of the small flatfishes, having a very delicate flavor . . . ."

LIFE HISTORY

Spawning and Larvae

The spawning of English sole has not been directly observed. All suggested spawning locations and times are inferred from the spatial and temporal distribution of either turgid or spent females or the egg and larval stages. The site of spawning is said to be over sand and sand-mud bottoms at depths of 60-110 m (Ketchen 1956; Barss 1976; Hewitt 1980). Spawning is usually most intense during winter (December to February), but is known to occur in all seasons; peaks vary from September to April (Laroche and Richardson 1979; Kruse and Tyler 1983). Individual English sole may spawn in more than 1 year, but probably do not spawn serially within a given season (Harry 1959; Kruse 1981).

There is no apparent latitudinal trend in the time of spawning (Laroche and Richardson 1979). However, Kruse and Tyler (1983) were able to develop a simulation model that explained most of the variation in observed spawning season. Their model was constructed from three relations between temperature and aspects of reproduction: (1) rate of gonadal development is inversely related to summer bottom temperature, (2) spawning is inhibited at temperatures below 7.8° C, and (3) spawning is delayed by rapid increase in bottom temperature.

Although English sole spawn demersally, their eggs are buoyant in full-strength seawater. Reported egg diameter varies from 0.89 to 1.05 mm (Budd 1940; Orsi 1968). Hatching time varies from 3.5 to 12 days and depends on both temperature and salinity (Alderdice and Forrester 1968; Orsi 1968). Orsi (1968) provided a detailed description of the embryology of the English sole that included a series of photos and illustrations of the egg and early larval stages. He noted that newly hatched larvae are 2.4-2.9 mm TL and grow to 4.6 mm during the 9-10 days (at 10.6 °C) of yolk-sac absorption. Orsi also noted that in the absence of food, the last surviving larvae died at 14 days.

The larvae of English sole are pelagic and depend on favorable current patterns for transport to suitable nearshore nursery areas. The duration of this pelagic larval stage is generally cited as 6-10 weeks (Ketchen 1956; Laroche et al. 1982). Transformation to asymmetrical morphology and settlement to a demersal existence coincide as the larvae reach 18-22 mm TL, at 60 to 120 days of age (Laroche and Richardson 1979; Rosenberg and Laroche 1982).

Postlarvae and Juveniles

English sole settling periods vary widely even at the same location. Krygier and Pearcy (1986) reported the capture of metamorphosing sole in Yaquina Bay, Oregon, from November through July; the month of maximum density varied from November to May. This protracted period of benthic recruitment may reflect the variability in the spawning season (Kruse and Tyler 1983).

Although it had been concluded in the past that estuaries alone serve as nursery areas for juvenile English sole (Demory 1979; Olson and Pratt 1973), new evidence suggests that shallow, open coastal waters may also provide juvenile rearing habitat (LaRoche and Holton 1979; Rosenberg 1982; Krygier and Pearcy 1986). Demory et al. (1973) listed ten Oregon estuaries occupied by juvenile English sole. Postlarval settlement occurs both in estuaries and along sand-bottomed open coastlines, primarily at depths of less than 16 m (Laroche and Holton 1979; Krygier and Pearcy 1986). Growth rate of post-settlement, 0-age English sole is comparable in estuaries and open coastal sites (Rosenberg 1982; Krygier and Pearcy 1986). The number of juveniles at open-coast sites, however, decreases sharply after initial settlement. It is not yet known to what extent this decrease is due to the migration of newly settled English sole from the open coast to estuaries (Krygier and Pearcy 1986) or to differential mortality.

Alternate hypotheses, both based in optimal foraging theory, have been presented to explain the distribution of postlarval and juvenile English sole within estuaries. Yoklavich (1982) suggested that the influence of temperature on growth rate may limit the distribution of juveniles to the cooler, deeper channels in more southern bays but favor a wider use of intertidal habitats in northern bays and estuaries. Toole (1980) proposed that the distribution of young English sole in Humboldt Bay could be explained as a combined response to predator and competition avoidance as well as optimal prey size availability. Given the scope of the hypotheses, both may be correct.

Juveniles move to progressively deeper waters with growth, and leave the nursery areas at 140-150 mm TL (Misitano 1976; Sopher 1974, as cited in Toole 1980). This emigration from the estuaries generally occurs from August through November (Pearcy and Myers 1973; Yoklavich 1982). Again, several alternative cues to emigration have been proposed, such as temperature by Yoklavich (1982) and niche

shift and competition avoidance by Toole (1980). Westrheim (1955) suggested that "perhaps less than 5% remain in the bay through the winter and presumably emigrate in the late winter or early spring of their second year."

Adults

Adult English sole are almost entirely absent from coastal bays and estuaries (Westrheim 1955; Misitano 1976), and are generally restricted to offshore sand or sand-mud substrates (Demory et al. 1976; Barss et al. 1977; Demory 1984). The depths at which they are most abundant vary from about 20-70 m in summer to 40-130 m in winter (Dow 1969; Barss 1976). This results from a seasonal bathymetric migration which is usually associated with a contranatant (against the current) movement to and more passive movement with the current when returning from deeper-water spawning grounds (Ketchen 1956; Forrester 1969a,b).

Male English sole mature at 2-3 years of age and females at 3-4 years of age (Ketchen 1956; Van Cleve and El-Sayed 1969). Harry (1959) reported that 50% of the males were mature at about 22 cm TL, and 50% of the females at 31 cm TL. A review by Gunderson and Dygert (1988) lists the age of 50% maturity for females as 4 years, and the average female length at 50% maturity in an unexploited population as 388 mm. Harry (1959) reported that the number of eggs per female ranged from 327,600 for a 30-cm fish to over 1.5 million for a 43-cm fish. On the basis of Harry's data, Demory (1984) calculated the following equation:

$$F = -1{,}875{,}906 + 75{,}377\ L$$

where: F = fecundity (number of eva)

L = total length (cm).

GROWTH

Rosenberg and Laroche (1982) detailed the growth pattern of larval, metamorphosing, and early 0-age English sole. There was a period of reduced growth rate during metamorphosis between 60 and 120 days of age and 18 to 22 mm standard length (SL). After growth was resumed, the newly recruited benthic specimens had reached about 34 mm SL at an age of 200 days (= 0.15 mm/day).

Rosenberg (1982) calculated a growth rate of 0.28 mm SL/day for English sole 140-480 days old. Krygier and Pearcy (1986) calculated a growth rate of 0.37-0.40 mm SL/day for fish of a similar size range at the same sites (Yaquina Bay and Moolach Beach, Oregon) and the same years (1978-79). Rosenberg's calculation was based on otolith aging techniques, and Krygier and Pearcy's on modal progressions of length-frequency data. Both reports, as well as that of Laroche et al. (1982), discussed the possible errors of each technique. Krygier and Pearcy (1986) also estimated that average daily growth of fish of this age group was greatest (0.46-0.49 mm) in late spring to early fall, and much lower in winter (0.26-0.32 mm).

English sole have been reported to attain 130-160 mm TL by the end of the first year of life (Van Cleve and El-Sayed 1969; Westrheim 1955; Smith and Nitsos 1969). Yoklavich (1982) compared the relative growth rates of laboratory-reared 0-age (72-114 mm SL) and "age class II" (156-188 mm SL) P. vetulus. For trials run at 13 °C, age 0 fish grew at a rate of 1.9% and age II fish at 0.8% body weight per day. Gross conversion efficiency, (total growth/total ration) in terms of both dry weight and calories, was greatly reduced for age II fish (12.1% and 17.8%, respectively) from efficiencies of age 0 fish (26.8% and 34.5%, respectively).

Growth rates of males and females are similar during the first 2 years (Barss 1976), but females grow faster thereafter. Van Cleve and El-Sayed (1969), who provided a broad review of several growth studies of English sole, included a listing of von Bertalanffy growth equation constants from their own and other studies. Although the relation of length to weight was not markedly different in males and females (Figure 3), a plot of length at age (Figure 4) clearly demonstrated their different growth rates, particularly as adults. Maximum total length and age is 57 cm and 17 years for females, 49 cm and 15 years for males (Forrester 1969a).

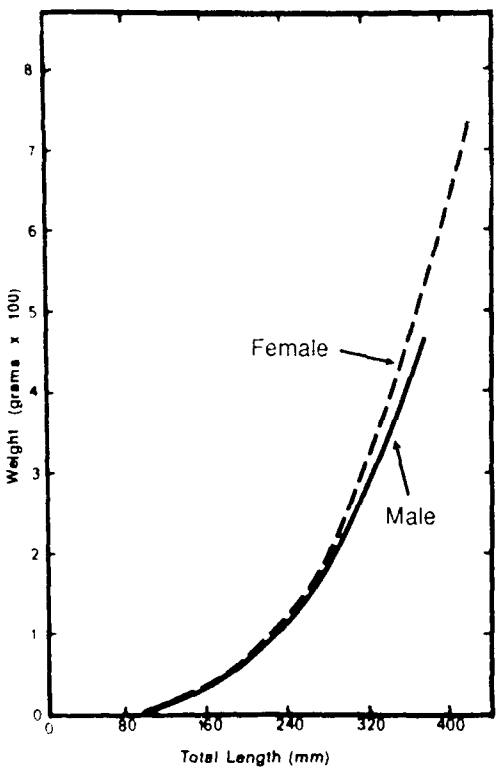

Figure 3. Length-weight relationship for Parophyrys vetulus; redrawn from Holland 1969).

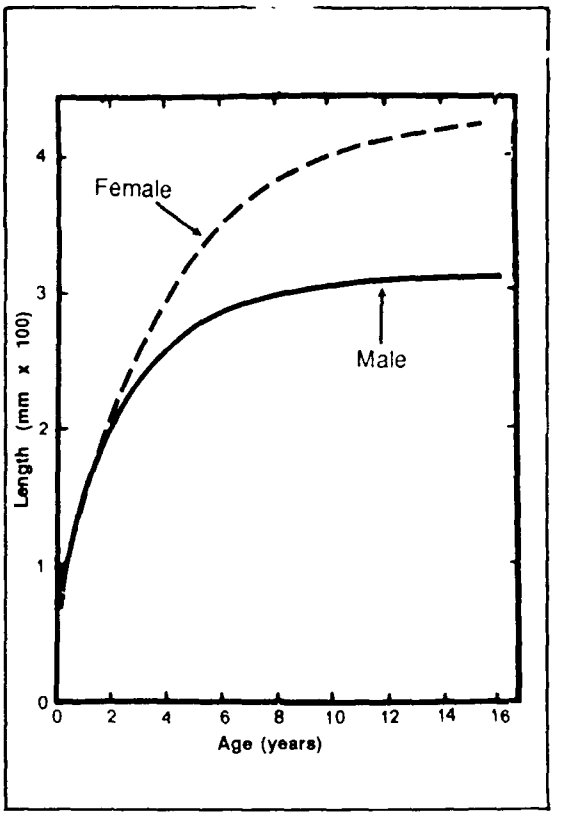

Figure 4. Length-age for English sole; redrawn from Van Cleve and El-Sayed 1969).

Kreuz et al. (1982) reported a March through September growing season for adult English sole, growth being most rapid in May and June. Growth rates between their study locations (Astoria and Coos Bay, Oregon) did not differ but did vary significantly among years. Fluctuations in annual growth increments were negatively correlated with a continental shelf temperature index (which increased with increasing temperature) for peak growth months and growth appeared to be related to long-term trends in upwelling. They also concluded that growth "does not seem to be associated with stock density." The relationship of growth and maturation in English sole may have changed in recent years

(Ellen Pikitch, Department of Fisheries and Wildlife, Oregon State University, Corvallis; pers. comm.), such that sexual maturity is now reached at a smaller size than was reported by Harry (1959; see Life History section).

MORTALITY

Mortality in English sole, as in nearly all fishes, is greatest during early life-history stages. Several researchers have correlated year-class strength with the extent and time of spawning and the successful benthic recruitment of pelagic egg and larval stages (Ketchen 1956; Hayman and Tyler 1980; Kruse 1984). Sources of mortality for eggs, larvae, and newly recruited juveniles include adverse temperature and salinity conditions (Alderdice and Forrester 1968), predation (Rosenberg 1982), adverse ocean advection (Kruse 1984), and absence of prey for larvae (Gadomski and Boehlert 1984).

Reported annual mortality rates for older fish are based largely on data from catches in experimental and commercial trawls. Mortality varies widely with sex, age, and the degree of exploitation. Average annual mortality may be as high as 50%-75% in highly exploited stocks (Ketchen 1947, as cited in Holland 1969; Menasveta 1958). Ketchen reportedly estimated annual natural mortalities in an unexploited population as 30% for females, and 38% for males. A coastwide rate of annual natural mortality of 23% was reported by the Pacific Fishery Management Council (1982). Barss (1976) reported a different pattern from exploited stocks off the Oregon coast, where mortality was higher in females (36%) than in males (32%). He suggested that the difference was due to the higher susceptibility of the larger females to commercial fishing pressure. An even more complicated picture was presented by Holland (1969). His investigations in Puget Sound showed a greater mortality for females (36%) than males (33%) from the third to fifth years of life at one site, but the reverse (males = 38%-50%, females = 27%-46%) for 8- to 10-year-old fish at a second site. Golden et al. (1986) used a value of 26% average annual fishing mortality to reconstruct stock sizes off the Oregon coast. They also estimated age-specific mortality values for fish from 3 to 13 years of age.

In a study of 20 different species of fish that included copper rockfish (Gunderson and Dygert 1988), the instantaneous natural mortality rates were positively correlated with the gonadosomatic index (GSI), expressed as gonad weight ÷ bodyweight. It may be possible for this index to predict the natural mortality rate for a fishery management model of English sole. Note that Gunderson and Dygert estimated GSI as 0.18 for this species.

MOVEMENT AND STOCKS

Knowledge of the discreteness of populations is integral to the management of any species. Except for brief mention by Clemens and Wilby (1961) that English sole "move about freely," most authors have concluded that movement is largely restricted to seasonal spawning migrations (previously discussed) in geographically segregated stocks (Ketchen 1956; Jow 1969; Pattie 1969; Barss 1976). There may, however, be a small but highly migratory fraction in many stocks, as reports on most tagging studies have mentioned at least one or a few long-distance recoveries. Migration rates have been as high as 4 mi/day (Hart 1973) and tag recovery distances as great as 700 mi (Clemens and Wilby 1961).

Major spawning populations within the Pacific Northwest region have been identified from Puget Sound (Holland

1969), the northern Washington coast (Pattie 1969), the central Oregon coast (Barss 1976), and two stocks in northern and central California that are segregated roughly in the vicinity of Eureka (Jow 1969). There is some indication of mixing near the prescribed boundaries of several stocks, as well as evidence of multiple substocks within the major groupings (Holland 1969; Forrester 1969b). Day (1976) concluded on the basis of tagging and recapture data that English sole in Puget Sound demonstrated "pronounced homing" and suggested that individuals may be territorial. However, I have found no record of behavioral observations to substantiate the possibility of territoriality.

DISEASE AND PARASITES

Olson (1978) reported on extensive studies of host-parasite relations in juvenile and adult English sole along the Oregon coast. The presence and intensity of infections were related to the habitats in which the fish were collected; infection was a more serious factor in habitats with higher temperature. A total of 29 species of parasites were identified. At temperatures above 15 °C, juveniles are apparently more susceptible to a microsporidial infection capable of causing mortality. Angell et al. (1975) determined that an epizootic skin tumor disease was a significant cause of mortality in a Puget Sound population of juvenile English sole.

A myxosporidean disease that causes a "milky" appearance to develop in the flesh of some adult English sole renders the fish unmarketable. A "wormy" appearance presents a similar marketing problem when adults are infected with the nematode Philometra americana (Holland 1969; Barss 1976). Although no mention was made of their effect on the health of the fish, neither of these conditions is harmful to human consumers.

THE FISHERY

The English sole has been an important species in California trawl fisheries since the late 1880's (Jow 1969) and a major contributor to both the Washington and Oregon trawl fisheries (Pattie 1969; Barss 1976). Landings in both the U.S. and Canadian fisheries increased during the years immediately after World War II (Ketchen 1956; Jow 1969). In U.S. waters, however, the catch declined somewhat with the rise in prominence of the Dover sole (Jow 1969). Both Dover and English soles are used in the filet of sole trade.

Females comprise over 90% of English sole landings (Kruse 1984; Golden et al. 1986). Many mature males, because of their smaller size (see section on Growth), are apparently discarded at sea (Barss 1976). In 1959-79, in Pacific Marine Fisheries Commission (PMFC) Area 3A, age-classes 4-7 averaged nearly 80% of the total landings by weight (Kruse 1984). Average weight of females for this area and period was 0.45 kg (Kruse 1984).

The total weight of English sole landed during the years 1966-85 in International North Pacific Fishery Commission (INPFC) Columbia area and PMFC Area 3B combined averaged nearly 1,300 t (Golden et al. 1986). However, only one of the last 5 years of this period has produced landings in excess of 1,000 t. A similar pattern of decline is seen in estimated biomass in these same areas. Golden et al. (1986) compared survey (catch, effort, and catchability) and virtual population analysis (VPA) estimates of English sole biomass. They "tentatively concluded" that VPA estimates, which were much lower than survey estimates (e.g., 1985, VPA = 3,030-3,572 t; survey = 5,634 t) were the better of the two.

Unfortunately, this leaves open the possibility that past estimates

were too high or that a significant amount of catch is unaccountable because of nondirected multispecific fisheries. Parental stock may have been reduced to a level at which fishing mortality adversely affects recruitment. If so, management options for stock rehabilitation (e.g., trip limits, area closures, mesh-size regulation) are limited due to this multispecific nature of the catch. English sole represent only 7% of the total catch for all Oregon trawl fisheries in which they are taken (Golden et al. 1986). Alternative means of explaining recent declines in recruitment based on environmental factors (Ketchen 1956; Hayman and Tyler 1980; Kruse 1984) have apparently not been applied to recent oceanographic data (Golden et al. 1986). **Growth of age I fish was shown to be negatively correlated with density of the age-I cohort and with bottom temperature. Both factors should be considered in models of English sole stocks (Peterman and Bradford 1987). A recent model of population dynamics of English sole off Washington and Oregon achieved best results when it incorporated the following: (1) the effect of ocean temperatures on time of spawning, egg hatching success, and fish growth; (2) density-dependent larval mortality; (3) age-dependent mortality of fish <4 years old; and (4) density-dependent growth of age 1 fish (Peterman et al. 1987). A management model would further need to incorporate long-term changes in growth schedules indicated by recent evidence (Peterman et al. 1987).**

ECOLOGICAL ROLE

Gadomski and Boehlert (1984) found in their study off the Oregon coast that "the diet of P. vetulus larvae is very specific; appendicularians (Oikopleura spp.) comprised 97% of the total number of food items consumed" when their peak abundances coincided. In that portion of the study when peaks did not coincide, appendicularians were still the primary food item (66%), but the diet also included "other food sources such as tintinnids, invertebrate eggs, and nauplii." These authors suggested that such apparent dependence on a specific prey "may result in significant food-related mortality" in years when larval and appendicularian peak abundances do not coincide. Hogue and Carey (1982), who examined the guts of 40 metamorphosing larvae (16-18 mm SL), found no evidence of feeding. This lack of feeding may help explain the occurrence of a "growth plateau" during metamorphosis (see section on Growth).

Both Hogue and Carey (1982) and Toole (1980) found that harpacticoid copepods were a major food source of early 0-age English sole. Hogue and Carey (1982) found that other small prey such as polychaete palps and juvenile bivalves were also important dietary items. After measuring the mouth size of specimens of 30 mm (SL), they concluded that prey of greater than 2 mm in any dimension were too large to be consumed. Both studies described a feeding transition within 0-age sole -- Hogue and Carey (1982) at 35 mm SL and Toole (1980) at 50-65 mm TL. This size range coincides very nearly with the change to "adult" morphology (Toole 1980).

Juvenile English sole are apparently opportunistic and generalist benthic feeders, with selection only at the level of major taxonomic groups of prey (Toole 1980). Within prey groups, the extent of dietary inclusion varies with local seasonal prey abundance (Collins 1978; Toole 1980; Hogue and Carey 1982). The most commonly mentioned prey items include polychaetes, amphipods, cumaceans, and bivalve siphons. Hogue and Carey (1982) described two patterns of feeding behavior in laboratory-held juveniles -- the first a sort of sit-and-wait strategy with occasional lunges at surface prey, and the second

a more active disturbance of the upper few millimeters of sediment and subsequent feeding on fleeing prey. In this same study, data on diel change in gut fullness suggested that juvenile English sole are primarily diurnal feeders.

Hulberg and Oliver (1979), who analyzed the taxonomic and "ecological" composition of the diets of adult English sole ($\bar{x}$ = 228 mm SL) and speckled sanddab (137 mm) from Monterey Bay, found considerable taxonomic overlap in their diets. However, behavioral and microhabitat differences among prey species and in feeding behavior of the two flatfishes suggested a clear trophic separation. The English sole fed primarily on shallow-burrowing, surface-active prey, but was apparently capable of digging into the sediment to capture deeper-burrowing prey as well. The sanddab limited its feeding primarily to hyperbenthic and pelagic prey. A detailed taxonomic and numerical description of the diet of large (230-450 mm TL) English sole and four other flatfishes from off the Oregon coast was presented by Kravitz et al. (1976). For the single day on which fish were collected, the diet of P. vetulus was the most diverse. Again, amphipods, polychaetes, and cumaceans were commonly consumed. Like the juveniles, adult English sole feed opportunistically on a wide variety of benthic invertebrates, such as polychaetes, shrimp, and small molluscs and crabs (Clemens and Wilby 1961). The polychaetes Capitella spp. are locally abundant in disturbed areas. In these areas, English sole exhibit significant numerical and size selection of this food. Frequency of Capitella spp. and median size were usually significantly greater in the fish than in the environment (Becker and Chew 1987). Feeding on this polychaete peaked at night, whereas adult English sole do not usually feed then (Becker and Chew 1987). Benthic assemblages dominated by pioneer species such as Capitella spp. may have comparatively high productivity and hence be an enhanced food source. It has not been established, however, that enhanced populations of a small number of species of prey will provide a healthy, balanced diet (Becker and Chew 1987).

Pelagic larvae are subject to heavy predation by appendicularians (Kruse 1984). Toole (1980) noted a lack of predators in the intertidal areas used most heavily by juveniles, but found a small English sole in the gut of a juvenile lingcod (Ophiodon elongatus) that was caught in a nearby estuarine channel. Other potential predators in these channels were rockfish, croakers, and sharks. Rosenberg (1982) suggested that a greater abundance of "large fish" represented a more substantial threat of predation in the open ocean than in estuarine waters. Roffe and Mate (1984) found that P. vetulus constituted about 5% of the diet of Pacific harbor seals in the Rogue River, Oregon. Seabirds (e.g., cormorants and pigeon guillemots) may also prey on juvenile sole.

ENVIRONMENTAL REQUIREMENTS

Temperature

Ames et al. (1978) determined an upper lethal temperature limit (50% survival) for P. vetulus of 26.1 °C. Juveniles of less than 119 mm were more susceptible than intermediate-sized fish. Yoklavich (1982) found a significant reduction in juvenile growth rate at 17.5 °C. Reduced relative growth rate was due to a decline in daily ration rather than in conversion efficiency. Yoklavich further related high temperatures to the distribution of juveniles within estuaries as well as their time of emigration from estuaries, particularly at the southern margin of their geographic range.

Lower lethal temperature limits have been addressed primarily for the

eggs of English sole. Ketchen (1956) observed complete mortality and no development past first cleavage at 3.8 °C. At 7 °C, eggs proceeded through several stages of development, but all died before hatching. Alderdice and Forrester (1968) observed complete mortality of eggs at 20 °C, but were able to attain a 50% hatching success at 4 °C. A 90% total hatch was estimated to occur in the temperature range of 7-11 °C. These authors concluded that temperature may limit abundance at the northern and southern boundaries of the range of commercial exploitation by lowering egg viability, and may be lethal to eggs near the boundaries of geographic distribution. Kruse (1984) used their temperature-hatch success relation and found it consistent with Oregon temperatures and year-class strengths.

Temperature has a marked influence on development time (Alderdice and Forrester 1968). Hatching occurred in only 3.5 days at 12 °C, but required 11.8 days at 4 °C. A similar slowing in the development of larval English sole at low temperatures is central to the explanation given by Ketchen (1956) for an observed inverse relationship between sea surface temperature and year-class strength. It has also been suggested that oceanic temperature during the pre-spawning period influences year-class strength (Hayman and Tyler 1980; Kruse 1984).

Salinity

I found no experimental information on the salinity tolerance of juvenile or adult English sole. However, Alderdice and Forrester (1968), who investigated the effects of salinity on hatching success, reported that a 90% total hatch was estimated to occur within a salinity range of 17-34 ppt. The breadth of this range led them to conclude that "over the geographic range of the species, salinity would appear to have little influence on egg viability."

Temperature/Salinity Interaction

Alderdice and Forrester (1968) found that the "interaction effect of temperature and salinity on total hatch is such that, with increases (or decreases) in salinity, maximum survival is maintained only with coupled increases (or decreases) in temperature." In their experiments, a temperature change of 1 °C was roughly equivalent (in effect on total hatch) to a salinity change of 4 ppt. They further concluded that optimum conditions for survival "appeared to be associated with salinities and temperatures of 25-28 ppt and 8-9 °C."

Other Environmental Factors

All demersal life stages are apparently associated with unconsolidated sediment substrates. Barss (1976) observed that laboratory-held juveniles bury themselves and concluded that they are thus limited to a sand bottom. Adults have been collected almost entirely from sand or sand-mud substrates (Barss 1976; Day and Pearcy 1978), though Ketchen (1956) reported that all English sole spawning grounds in his study were over "soft mud" bottoms.

I found no information on experimentally determined dissolved oxygen minima for juvenile or adult English sole. However, Levings (1980) caught decreasing numbers of English sole from a British Columbia fjord during a period in which dissolved oxygen levels dropped to 1.0 mg/l. After this point, P. vetulus was no longer caught. It was not known whether this was due to emigration or to mortality. Alderdice and Forrester (1968) concluded that "oxygen is not likely to be a critical factor" in the survival of pelagic eggs and larvae.

Fairly extensive information about the effects of contaminants on English sole is available (Krahn et al. 1984; Malins et al. 1984). Johnson et al. (1988) report that exposure to aromatic

hydrocarbons may interfere with ovarian development.

AREAS OF CONCERN

Perhaps the most critical area of concern in the biology of the English sole is in developing an understanding of recent declines in recruitment. Such an effort would require the verification of causal mechanisms suggested by Ketchen (1956; on interaction of temperature and water currents during the larval stage), by Hayman and Tyler (1980; on prespawning temperature conditions), and by Golden et al. (1986; on overexploitation of parent stock). A clarification of population dynamics (particularly mortality) in open coastline versus estuarine nursery areas is also needed. Of particular concern to coastal development is the possibility, particularly at the southern margin of English sole distribution, of thermal pollution altering the suitability of existing estuarine nursery areas.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, distribution, life history, ecological role, and environmental requirements of coastal aquatic species. They are prepared to assist coastal managers, engineers, and biologists in the gathering of information pertinent to coastal development activities. The English sole is a major contributor to Pacific Northwest trawl fisheries and is used extensively in the filet-of-sole trade. Spawning is usually most intense during winter, but occurs in all seasons. Temperature conditions before spawning and during the egg and larval stages are critical to subsequent year-class strength. Hatching success is apparently greatest at salinities and temperatures of 25-28 ppt and 8-9 °C. Postlarvae settle in open-coast and estuarine areas. Densities of rearing juveniles are highest in lower estuaries. Growth may be inhibited at temperatures above 17.5 °C. Emigration from nursery areas to deeper, sand-bottomed offshore areas occurs during late summer and fall. Juveniles and adults feed on a wide variety of benthic invertebrates. Female English sole grow faster and mature later (3-4 years) than males (2-3 years). Females are more susceptible to capture in the multi-species trawl fisheries that typify Pacific Northwest ground fishing. A better understanding of the relation between oceanic conditions and early life-history stages, the avoidance of estuarine thermal pollution, and the protection of remaining coastal nursery areas are important to the maintenance of English sole abundance.

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